

Foragers of the Harvester Ant, *Pogonomyrmex owyheei*: A Disposable Caste?

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Summary. 1. Exterior workers of the harvester ant, *Pogonomyrmex owyheei*, were subdivided into forager, defender and refuse worker behavior roles (Fig. 2). Exterior workers comprised approximately 16% of the total colony population with interior workers comprising the remainder.

2. An average of less than 10% of the total worker population foraged (Table 1). Studies of role changes confirmed a general one-way progression from interior workers to defenders to foragers (Fig. 5). The average longevity of foragers was about 14 days. As interior workers progressed toward foraging, their dry weights declined approximately 40% (Fig. 3) and mandible wear increased (Table 2).

3. Based on these results, we propose that *P. owyheei* has evolved a disposable forager strategy that tolerates high forager mortality. The large reservoir of interior workers required by this strategy may also inhibit the evolution of physically specialized interior worker castes.

Introduction

When ants evolved from the solitary mode of existence and adopted sociality (Wilson 1971), they increased their susceptibility to predation. Formation of social groups made ant colonies essentially stationary food resources for predators. Next, the development of overlapping generations extended colony longevity from weeks to years, making some colonies exceptionally stable sources of food. Larger colony sizes further increased potential for predation since larger colonies represented easily located, richer and more concentrated food sources. When these evolutionary changes are combined with high colony density, ants become ecological equivalents of dominant

perennial vegetation; in that both are stationary, dependable and easily located food sources, or what Feeny (1976) described as 'apparent' species.

The harvester ant, *Pogonomyrmex owyheei*, is an example of an 'apparent' species. Mature colonies are clearly marked by large mounds surrounded by clearings averaging 3 m in diameter (Willard and Crowell 1965). Colony densities in Oregon and Idaho often exceed 50 mounds/ha (Sneva 1979; Jorgensen 1979), with an average population of about 2500 ants/colony (Jorgensen 1979). In southern Idaho, colony longevity probably exceeds 10 years (calculated from Sharp and Barr 1960) with surface activity continuing from late May through early August. These characteristics would seemingly make *P. owyheei* a readily accessible food source for predators.

The literature suggests that *Pogonomyrmex* ants are indeed utilized as food by a number of predators including birds, lizards, spiders and wasps (Gentry 1974; Knowlton 1974a, b; Pianka and Parker 1975; Clark and Comanor 1975; Hölldobler 1970; Evans 1962). Sage sparrows, lizards and several species of spiders were observed preying on *P. owyheei* foragers during our studies. One spider, *Euryopsis coki*, appeared to specialize on these ants (Porter and Eastmond, in press). Unfortunately, our data do not allow us to quantify effects of these predators on *P. owyheei* populations. Whitford and Bryant (1979), however, estimated that the horned lizard, *Phrynosoma cornutum*, consumed approximately 72% of all *Pogonomyrmex* workers produced each year at a site in New Mexico.

If *P. owyheei* is subjected to heavy predation because of high 'apparency', we expect that defensive adaptations would be necessary to ensure colony survival. (1) The sting is probably the most obvious and effective defensive adaptation, especially against vertebrate predators (Schmidt and Blum 1978). (2) Deep subterranean nest construction may be another de-

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fense which protects the queen and much of her brood from easy access. (3) Clearing vegetation from around the nest may also protect the colony by excluding many arthropod predators from the immediate mound area where cover is not available (Clark and Comanor 1975), while subjecting vertebrate predators to increased predation themselves. (4) Gentry (1974), in his study of simulated predation, reported that a strong division of labor between interior and exterior workers may protect the colony by limiting predation to the small percentage of exterior workers.

Our data suggest a fifth defensive strategy – that the social structure of *P. owyhee* is adapted to tolerate high forager mortality by the evolution of a disposable forager population consisting of low cost, short-lived workers. The purpose of our research was to examine this hypothesis.

Materials and Methods

Study sites were located in Raft River Valley, Idaho in cold desert sagebrush-greasewood (*Artemisia tridentata*-*Sarcobatus vermiculatus*) plant communities. Data were collected from May to August, 1977–1979. Seeds from Tansy mustard (*Descurainia richardsonii*), shield-crest (*Lepidium perfoliatum*) and squirreltail grass (*Sitanion hystrix*) were the primary summer forage for *P. owyhee*. A more thorough description of the study sites and their ecology was given by Jorgensen (1979).

Estimating Socially Stratified Populations. Workers were divided into five major behavior roles for studies of colony social structure: (1) *Foragers* – ants found 1 m or more from the mound on foraging trails. (2) *Refuse workers* – ants found carrying refuse from the mound entrance. (3) *Defenders* – ants that emerged from the mound after a general defense response was initiated by blowing into the entrance hole through an aspirator containing captured ants. (4) *Interior workers* – ants not active in exterior behavior roles. (5) *Callow workers* – newly eclosed ants of yellowish color. Since interior workers and callow workers could not be routinely captured and recaptured without partial excavation of the mound, they were excluded from mark-recapture experiments used to assess social structure. 'Exterior workers' include all workers performing at least a portion of their duties outside the nest. 'Dark workers' include all fully sclerotized workers in the colony, both interior and exterior.

Ants in our mark-recapture experiments were spray-marked with different colors of fluorescent felt-tip pen ink (Fluorescent Magic Marker® Studio Liners, Magic Marker Corp., Glendale, NY 11227, USA) or fluorescent printing ink (Day-Glo® Fluorescent 'Super' Bases, Gans Ink Co. of Utah, 1919 West 2300 South, Salt Lake City, UT 84119, USA) and viewed under a black light for mark detection. As described by Porter and Jorgensen (1980), both inks provided distinct marks that persisted several months in laboratory colonies without affecting mortality.

The Lincoln index as modified by Bailey (1951) was used to approximate the number of workers performing designated behaviors over a 24 h period. This index, however, was not suitable for estimating the number of ants performing a behavior at any one time because workers frequently shifted behaviors. Schaefer (1951), faced with a similar problem, used a stratified mark-recapture method which allowed him to estimate the number of salmon passing a particular point on the river each week. Chapman and Junge (1956) and Darroch (1961) analyzed Schaefer's

method and concluded it was applicable to spatially as well as temporally stratified populations.

We extended Schaefer's (1951) method to include behaviorally stratified populations of harvester ants. Capture data were arranged in an R_{ij} table (Fig. 1), and an estimate (N_{ij}) calculated for each cell using the formula

$$N_{ij} = R_{ij}(M_i/R_i)(C_j/R_j)$$

where:

R_{ij} = number of ants marked performing the i^{th} behavior and recaptured performing the j^{th} behavior,

R_i = sum of recaptures marked in the i^{th} behavior,

R_j = sum of all recaptures in the j^{th} recapture sample,

M_i = number of ants marked in the i^{th} mark sample, and

C_j = number of ants captured in the j^{th} recapture sample.

Both row ($N_{i.}$) and column ($N_{.j}$) sums for a given behavior in the N_{ij} matrix (Fig. 1) are stratified estimates of the number of ants performing that behavior at a given time. We averaged these corresponding estimates. The grand total of this matrix ($N_{..}$, Fig. 1) is an estimate of the combined population and is mathematically equivalent to a composite or combined Lincoln index estimate calculated after summing across behaviors (see Table 1). Assumptions of random mixing and equal sampling effort may be questioned in our use of both the Lincoln index and the Schaefer estimator, but we feel these questions are not particularly serious as long as the resulting estimates are considered relative approximations.

Social Structure. Schaefer's (1951) stratified mark-recapture method was used to investigate the social structure of exterior workers, particularly their population sizes and behavior interrelationships. Five behaviors were sampled at four large mounds in late June, 1979: F_1 –foragers on the main trail, F_2 –foragers on minor trails, R –refuse workers, D_1 –first defenders and D_2 –second defenders. Samples of first and second defenders were about equal in size but segregated arbitrarily according to their order of emergence. Each group was distinctly marked with printing ink and recaptured 24 h later.

In order to correlate the size of exterior worker populations with total colony size, forager and defender populations at 12 mounds were estimated several times. The mounds were then excavated using a backhoe (Lavigne 1969) soon after the last mark-recapture period. Four mounds were excavated in June, three in July and five in early August 1978. Foragers, defenders and all remaining ants uncovered during the excavation were captured and frozen, grouped by behavior and/or depth of capture. They were subsequently checked for fluorescent marks and sorted into dark workers, callow workers and brood.

Morphological dynamics related to the respective worker behaviors were examined by measuring several morphological and weight characteristics. Body size and dry weight were examined by collecting 25 dark workers from each group of ants captured from the 12 excavated mounds. These ants were dried at 75°C for 24 h and weighed. The lightest and the heaviest groups of workers from each mound were then measured across the eyes to determine their average head widths. Head widths were obtained to assess the presence or absence of physically distinct castes (Wilson 1953).

Another more comprehensive study of morphological dynamics was made using 20 foragers, refuse workers, defenders, interior workers and callow workers from each of five additional colonies. Head width, wet weight, dry weight and mandible wear for each ant were obtained. Mandible wear was assessed on a scale of 0–3, with 0=no recognizable wear and 3=completely flattened teeth (Higashi 1974).

Starvation mortality studies (Weir 1958) were used to assess

usable energy reserves of foragers, refuse workers, defenders, interior workers and callow workers. Thirty ants exhibiting each behavior were collected from five mounds and marked with pen ink. They were then regrouped by mound and released into sealed plastic containers with moist plaster-of-paris bottoms. These ants were retained without food for 37 days, with dead ants being removed periodically and sorted according to their original behavior to assess which group contained the greatest energy reserves.

Foraging Dynamics. Role change and field mortality studies were undertaken to investigate the population dynamics and foraging costs of *P. owyheeii* colonies. Role change and mortality of surface active ants were studied by monitoring changes in the frequency and distribution of marked ants in forager and defender recapture samples taken over a three week period. All possible foragers and defenders at each of five mounds were captured and marked with pen ink. Defenders were stratified into two or three subsamples by order of emergence and marked accordingly. Subsequently, small forager (~100) and defender (~150) recapture samples were collected, counted and released every second or third day at two of the five mounds. The remaining three mounds were sampled several times, but only at the beginning and end of the recapture period.

Results

Social Structure

Exterior Behaviors. An explanation of *P. owyheeii* foraging strategies is dependent on a rather complete knowledge of worker role fidelity and population dynamics. The population size and interrelationships of exterior worker behaviors are of particular importance. χ^2 analysis of pooled mark-recapture data from four large mounds confirmed that social structure of exterior workers was distinctly stratified ($\chi^2 = 995.7$, 16 d.f., $P < 0.001$). These pooled results indicated that with the exception of first defenders, ants marked performing specific behaviors were more likely than expected to continue performing those same behaviors (diagonal cells in R_{ij} matrix, Fig. 1). Again with the exception of first defenders, exterior workers were less likely than expected to shift either into or out of the main trail forager role (row one and column one, R_{ij} matrix, Fig. 1), indicating that these foragers form a sub-population segregated from other exterior workers. χ^2 analyses for the individual mounds provided patterns similar to those illustrated for the pooled results (Fig. 1).

Stratified estimates of exterior workers in the four large mounds (Fig. 1) averaged 380 foragers ($F_1 + F_2$), 100 refuse workers and 632 defenders ($D_1 + D_2$), indicating that during the hours of foraging, approximately 10% of exterior ants were performing refuse work, 35% were foraging and 55% were available for defense. Lincoln index estimates averaged 610 foragers, 244 refuse workers and 945 defenders, indicating that over a 24 h period approximately 20% of exterior

R_{ij}		Mark Samples (i)					$R_{.j}$ C_j	
		Forager ₁	Forager ₂	Refuse	Defender ₁	Defender ₂		
Recapture Samples (j)	F_1	77	1	3	22	9	112	172
	F_2	2	17	5	13	14	51	78
	R	2	2	17	14	13	48	76
	D_1	22	12	13	44	52	143	194
	D_2	14	5	7	24	47	97	234
	$N_{.j}$	117	37	45	117	135	451	754
		M_1	180	58	57	173	197	665

N_{ij}		Mark Estimates (i)					$N_{.j}$	
		Forager ₁	Forager ₂	Refuse	Defender ₁	Defender ₂		
Recapture Estimates (j)	F_1	182	2	6	50	20	260	
	F_2	5	41	10	29	31	116	
	R	5	5	34	33	30	107	
	D_1	46	26	22	88	103	285	
	D_2	52	19	21	86	165	343	
	$N_{.j}$	290	93	93	286	349	1111	

Fig. 1. Cell by cell averages of stratified mark-recapture data from four large mounds (R_{ij}), and corresponding Schaefer estimates (N_{ij}). Those cells contributing prominent values (> 20) in a pooled χ^2 -test are stippled to show negative deviations or hatched to show positive deviations

workers performed refuse work, 55% foraged and 85% could defend.

A transition diagram (Fig. 2) using the stratified estimates in Fig. 1 helps to illustrate the short-term social structure of exterior workers. It is apparent from Fig. 2 that although workers readily shifted between behaviors, they often retained strong fidelity for a particular behavior. This figure, combined with the preceding χ^2 analyses (Fig. 1), indicates that first defenders (D_1) were largely a mixture of ants from the other four behavioral groups; that is, workers captured as first defenders readily shifted into and out of the other roles without showing a significant tendency to persist as first defenders. This flexibility suggests that first defenders were either a composite of the other behavioral groups or a transitional stage between foragers and second defenders. Second defenders (D_2) also contained a fairly large number of ants from the other behaviors; however, a large percentage of them persisted as second defenders. The

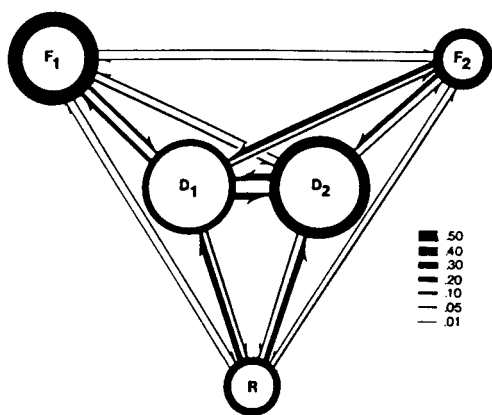


Fig. 2. Transition diagram for five exterior behaviors displayed by *Pogonomyrmex owyhee* workers (see Fig. 1). Width of lines is proportional to the probability of transition (arrows) or non-transition (circles) 24 h after marking. Circle areas are drawn to scale and represent the mean population of workers performing a given behavior (transition probabilities were derived from Schaefer mark-recapture estimates, Fig. 1)

high interaction between first and second defender roles was not unexpected because our segregation during sampling was somewhat arbitrary. Few workers shifted between main trail foraging (F_1) and minor trail foraging (F_2), reconfirming the conclusion that harvester ant foragers have high route fidelity over a 24 h period (Hölldobler 1976; Porter and Jorgensen 1980). Interior behaviors performed by exterior workers were not examined in our sampling; thus we could not determine if specific exterior behaviors were primary or secondary roles of the workers.

Colony Excavations. An average of 27% of the workers recovered from the 12 excavated colonies were found in the mounds: the remaining 73% were collected below mound level – 36% at 0–30 cm, 14% at 31–60 cm, 11% at 61–90 cm, 8% at 91–120 cm and 4% deeper than 121 cm. Marked foragers and defenders were not recovered more than a few centimeters below mound level even 2 weeks after their release, suggesting that exterior workers rarely mix with the larger interior worker population. Erickson (1972) and Golley and Gentry (1964) also reported that marked *Pogonomyrmex* exterior workers rarely dispersed below mound level.

Mark-recapture results from the 12 mounds showed that defender, forager and their combined population estimates were strongly correlated with the total excavated worker population (Table 1). Schaefer defender and forager estimates averaged 11% and 6% of the total colony population, while Lincoln defender and forager estimates averaged 13% and 9%, respectively. Combined forager and defender

mark-recapture estimates indicated that approximately 16% of a colony was active on the exterior while 84% was not. Lincoln index estimates were more closely correlated to total colony size than were Schaefer estimates (Table 1). This difference may reflect chance, or perhaps the total number of potential foragers or defenders performing a job over a 24 h period (Lincoln estimate) was more closely related to total colony population than was the actual number of workers foraging or defending at any given time (Schaefer estimate).

Morphology Dynamics. Body size of *P. owyhee* was not correlated with the social structure of dark workers. Mean head widths of defenders and interior workers taken from the 12 excavated colonies were found not to be significantly different ($F_{1,576}=0.40$, $P>0.05$) using a 2-way analysis of variance. Likewise, foragers, refuse workers, defenders and interior workers from the five mounds studied more intensively (Table 2) failed to show significant differences in head widths. It appears from these data that *P. owyhee* is a monomorphic species without obvious tendencies towards polymorphism.

While body size was not correlated with social structure, body weight was. Mean dry weight of dark workers from 10 of the 12 excavated colonies declined approximately 40% along a gradient from interior workers to defenders to foragers (Fig. 3). The two excavated colonies with the lowest worker dry weights were also the two colonies with the smallest worker populations (Table 1). Gentry (1974) reported that dry weight of *Pogonomyrmex badius* workers in low predation test colonies declined 21% on a gradient from interior workers to exterior workers. He also reported that dry weights of workers in test colonies under heavy simulated predation declined only 6% along the same gradient. These results suggest that the two smaller colonies in Fig. 3 may have been under more environmental stress than the larger and presumably more permanently established colonies.

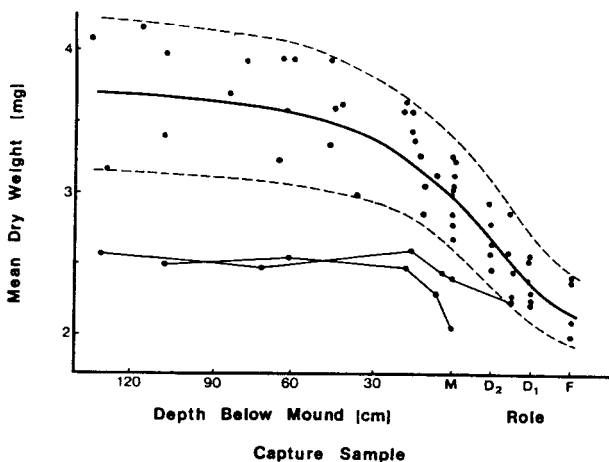
Wet and dry weights reported in Table 2 also decreased along the gradient from interior workers to foragers, declining 14% and 25%, respectively. Mean water content (wet weight minus dry weight) was fairly constant across dark worker behavior roles (Table 2) despite declining dry weight. These data, combined with those from Fig. 3, indicate that energy reserves decline as ants progress from interior worker to foraging. Interior workers apparently serve as a reservoir of colony energy while exterior workers appear to be drained of most usable energy in preparation for foraging.

Results of the starvation mortality experiments show that starvation mortality (Fig. 4) was inversely

Table 1. Correlations of total excavated *Pogonomyrmex owyheei* worker populations to Lincoln and Schaefer estimates. Forager and defender populations were estimated either once or twice at each mound

Mound	Total worker population	Lincoln estimates			Schaefer estimates		
		Defender	Forager	Combined	Defender	Forager	Combined
Excavated June 8–12							
1	6,371	650 831 ^a	493	669	464	206	669
2	1,581	178 134 ^a	110	182	112	68	180
3	1,850	374 220 ^a	225	430	252	176	429
4	831	55	77	108	47	62	109
Excavated July 12–17							
5	3,014	374 503	277 269	477 579	244 419	234 161	478 580
6	1,828	233 227	189 135	329 231	174 150	152 82	325 232
7	759	187	76	205	161	44	205
Excavated August 1–5							
8	1,605	156 ^a					
9	2,166	337 231	173 155	365 297	285 203	78 92	363 295
10	3,812	600 ^a 457 ^a					
11	2,764	473 356 ^a	300	497	358	139	498
12	2,383	353 260 ^a	255	304	170	135	305
Means	2,414	342	210	359	234	125	359
% Total worker population		13.3	9.1	16.3	10.6	5.8	16.3
Correlation with total worker population (<i>P</i> < 0.01)		0.92	0.95	0.85	0.82	0.69	0.85

^a Only the defender population was estimated



related to dark worker dry weight (Table 2). Foragers died first, followed in sequence by defenders, refuse workers and interior workers. Callow workers died at a rate slower than their dry weights (Table 2) suggest they should (Fig. 4), possibly as a result of a lower metabolic rate.

Mandible wear increased along the gradient from interior workers to foragers (Table 2), indicating that

Fig. 3. Mean dry weight of *Pogonomyrmex owyheei* dark worker samples from 12 excavated colonies graphed against worker roles and depths below mound. *F* foragers; *D*₁, *D*₂ first and second defenders; *M* ants removed from mound. Dashed lines indicate range of mean worker weights for the 10 medium to large sized colonies

Table 2. Morphology dynamics and their association with *Pogonomyrmex owyhee* social structure. Data are from five mounds. Dark worker means which are not significantly different ($P > 0.05$) in Duncan's range test are connected by lines. Callow worker means are shown for comparison

Physical factors	Means by behavior role				
	Forager	Refuse	Defender	Interior	Callow
Head width (mm)	1.85	1.84	1.85	1.85	1.88
Weight (mg)					
Wet	6.20	6.60	6.63	7.21	7.61
Dry	2.54	2.76	2.72	3.38	2.90
Water	3.66	3.84	3.91	3.84	4.71
Mandible wear	1.99	1.73	1.49	0.74	0.00

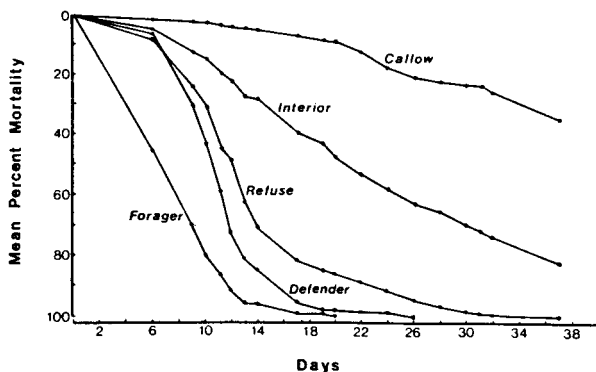


Fig. 4. Mean percent starvation mortality of forager, refuse, defender, interior and callow worker samples from five *Pogonomyrmex owyhee* mounds

this wear may be age and/or activity related. Foragers averaged moderate wear, followed closely by refuse workers and defenders. Mandibles of interior workers averaged only slight wear and those of callow workers had none.

Defenders and refuse workers were not significantly different in any of the morphological factors measured (Table 2), suggesting that refuse workers are a subset of defenders, specialized in removing rocks and chaff from the mound entrance. Although not as evident, a similar conclusion is suggested by analysis of short-term transition behavior (Fig. 2). Seed and chaff manipulation may in fact be the primary role of all defenders with the defense response being only an ancillary behavior.

Foraging Dynamics

Role Change. Analysis of two mounds intensively sampled every second or third day affirmed that individuals progress from interior workers to defenders to foragers (Fig. 5). Marked foragers recaptured while foraging declined to extinction in about 18 days. First defenders recaptured while foraging initially increased in frequency and then began declining. As first defenders declined, the frequency of second and third defenders in the foraging recapture sample began increasing. The frequency of unmarked ants captured while foraging increased slowly at first, and then rapidly as all marked defenders began declining.

In the defender recapture samples (Fig. 5), all four marked groups declined steadily after day four. Second and third defenders, however, declined more slowly than marked foragers and first defenders, suggesting that they did not transfer into the forager population as quickly. Unmarked ants were consistently more common in the defender recapture samples than in the forager samples, indicating that unmarked ants progressed first to defending and then to foraging. The sharp decline in marked foragers recaptured while foraging on day seven of mound B resulted from the mass recruitment of third defenders to a new foraging trail, thus diluting the frequency of marked foragers. While these data confirm a general progression from interior workers to defenders to foragers, this progression is not necessarily obligatory. That is, some workers may skip the defender phases completely while other workers may remain as defenders until death. Inspection of the recapture results from three mounds sampled only at the beginning and end of the sampling period showed the same basic trends, although in less detail.

Field Mortality. The percentage of marked foragers and defenders recovered from the 12 excavated mounds declined as a function of the time elapsed between marking and excavation ($y = 88 - 6.0x$, $r = -0.85$, $P < 0.001$) with the regression line reaching extinction about 14 days after marking. Marked foragers averaged slightly lower recovery rates than marked defenders but not significantly so when tested with a paired t-test ($P > 0.05$). Since mark loss and mark induced mortality were unlikely (Porter and Jorgensen 1980), these analyses suggest that exterior workers had an average life expectancy of about 14 days. Life expectancy of the foragers is important to the foraging strategy since it provides a principal element controlling the rate at which workers are recruited for foraging and establishes a minimum reproductive rate necessary to keep the colony viable and growing.

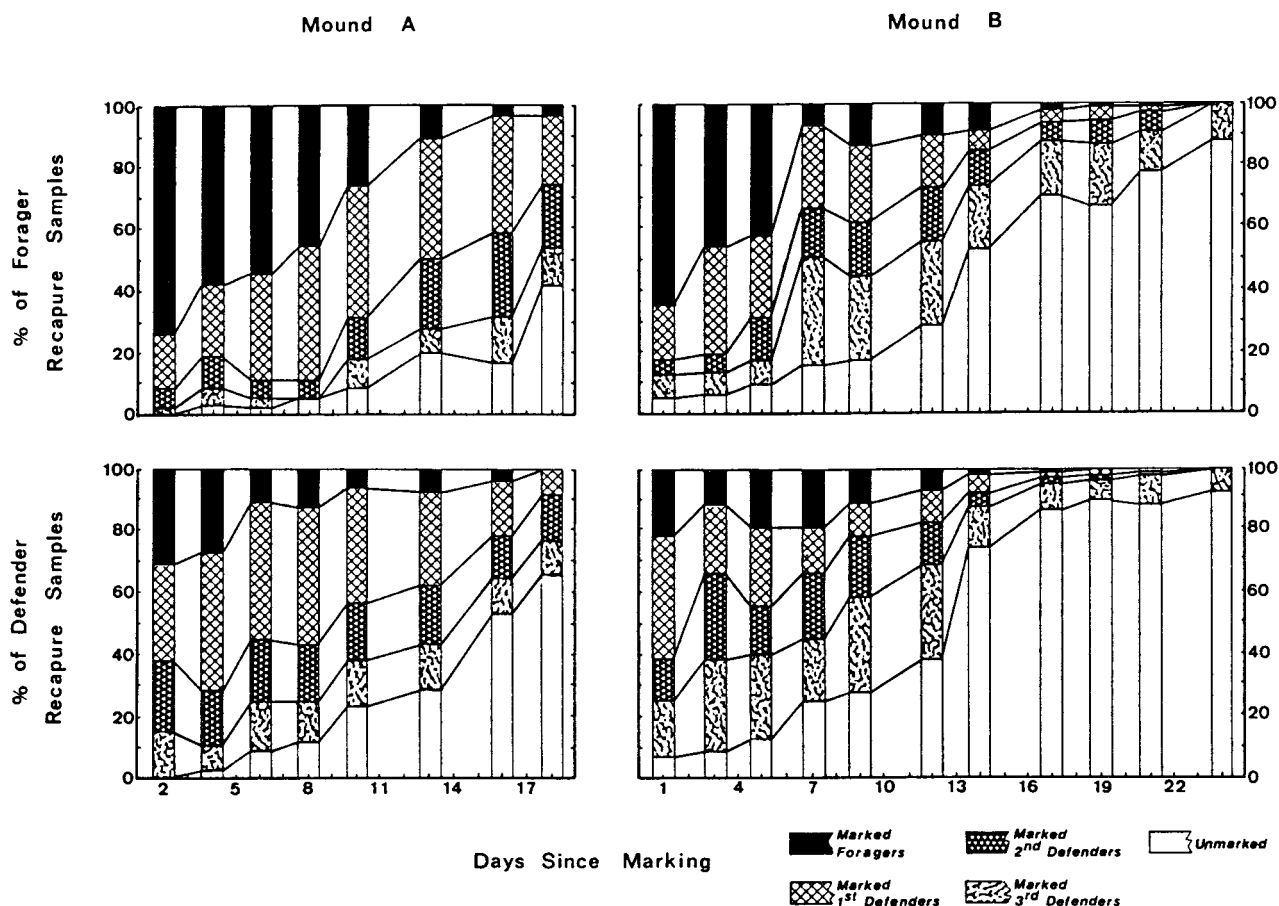


Fig. 5. The change over time in the composition of marked ants captured at mounds A and B in forager and defender recapture samples. The number of foragers, first defenders, second defenders and third defenders marked for each colony were respectively: 569, 550, 512 and 295 at mound A and 336, 258, 144 and 265 at mound B. First, second and third defenders were segregated arbitrarily by order of emergence

Comparison of the change over time in recapture frequency of marked foragers from all five mounds in the role change study corroborated 14 days as the average life expectancy of foraging workers. Marked foragers recaptured while foraging declined to zero in about 18 days with an average half-life of 7 days (range 5–9). Marked foragers recaptured while defending also declined to zero in about 18 days. Two of the mounds were partially excavated after the recapture period, but marked ants had not dispersed below mound level; thus dilution of marked workers into the total colony population was eliminated as a possible explanation for the loss of marked ants.

Discussion

Social Structure and Morphology Dynamics

P. owyhee colonies were stratified into interior and exterior worker populations. Exterior workers com-

prised approximately 16% of the total adult population with interior workers comprising the remainder. Exterior workers consisted of three overlapping populations: foragers, defenders and refuse workers (Fig. 2). Foragers were further stratified by foraging trails while defenders were stratified by their order of emergence. Less than 10% of a colony foraged, with only about 6% foraging at any given time (Table 1). Perhaps higher percentages of colony population could be recruited as foragers following discovery of a rich food source, but our highest forager populations were 13.8% (Lincoln estimate) and 9.5% (Schaefer estimate).

Whitford and Ettershank (1975) reported information indicating that large proportions of *P. rugosus* workers are occasionally involved in foraging. Whitford (personal communication) suggested that this behavior may be an adaptation for utilizing highly unpredictable food resources during periods of peak food availability. However, a review of literature con-

cerning other *Pogonomyrmex* species supports a general observation that only a small fraction of workers actually forage: *P. badius*–10% (Golley and Gentry 1964), 10–15% (Gentry and Stiritz 1972); *P. californicus*–11.5% (Erickson 1972); *P. occidentalis*–10% (Rogers et al. 1972). Data for other genera of ants are somewhat scarce, but again suggest that forager populations are often only a fraction of total colony population: *Atta cephalotes*–6.1% (Lewis et al. 1974), *Formica polyctena*–24.8% (Kruk-de Bruin et al. 1977), also see Ayre (1962), Mirenda (1981) and Traniello (1977).

Body size as measured by head width was not associated with *P. owyhee* social structure (Table 2), but body weight was. Dark worker body weights declined approximately 40% on a progression from interior workers to foragers (Fig. 3). Starvation mortality rates were inversely related to dark worker body weights (Fig. 4) suggesting that worker energy reserves decline as they progress to foraging. In similar starvation tests, Weir (1958) reported that *Myrmica rubra* foragers died more quickly than interior workers, and Rosengren (1977) reported that old *Formica rufa* foragers died more quickly than young foragers. These data suggest that available energy reserves of ants from other genera also decline as they progress to foraging.

Brian and Abbott (1977) studying *M. rubra* reported a hunger gradient that caused food flow from exterior workers to interior workers. A similar hunger gradient in *Pogonomyrmex* colonies may cause the weight gradient from interior to exterior workers which we have described. Energy, possibly in the form of fat reserves or enlarged ovaries (Wilson 1971), appears to accumulate in the deeper colony populations where ground temperature and respiration losses would be lower. Larvae and pupae produced at deeper levels weighed consistently more than those found at higher levels (unpublished data), possibly accounting for some intracolony worker size variation. Worker energy reserves may also be important to colony life cycles. For instance, production of reproductives could possibly be stimulated or inhibited by the extent of worker energy reserves. Also, the depletion of these reserves beyond a certain point might be a factor which stimulates individual ants to begin foraging.

Mandible wear also increased on a progression from interior workers to foragers. The mandibles of some individuals became so worn that they no longer met when closed and could not hold small items. Wear on body sensillae may also be correlated with mandible wear; if so, many exterior workers may have lost a large portion of their sensory capabilities. Stoffolano (1973) reported that 30–50% of adult

blowfly labellar chemoreceptors were inoperative 25 days after eclosure. Dethier (1976) suggested that this reduction in sensory capabilities may explain why feeding among aging blowflies is markedly reduced. A similar reduction in sensory capability of aging *Pogonomyrmex* workers could explain why a large proportion of foragers return empty or carrying inedible detritus (Willard and Crowell 1965; Rogers 1974; Jorgensen and Porter, in press).

Foraging Dynamics

Our role change studies established a general progression from interior workers to defenders to foragers with the forager role terminating in death (Fig. 5). The average longevity of a foraging worker was approximately 14 days (Porter and Jorgensen, 1980, Fig. 5). Since observed field mortality approximates starvation mortality (Fig. 4), it seems that exterior workers may consume little food during the remainder of their life. Wilson and Eisner (1957) reported that sugar transmission among *P. badius* workers is almost zero, and that trophallaxis between workers had not been observed. Oster and Wilson (1978) hypothesize that physiological senescence will evolve to approximate natural mortality rates. Starvation mortality of *P. owyhee* may support their hypothesis.

Four factors may contribute to the high mortality rate of foraging workers: (1) Foragers may die as a result of predation pressure facilitated by the 'apparent' nature of *Pogonomyrmex* populations. Whitford and Bryant (1979), as previously mentioned, reported that in New Mexico 72% of total colony population was consumed by horned lizards during the course of a year. (2) Some ants may die as a result of intercolony aggression. Although we did not observe this phenomenon with *P. owyhee*, De Vita (1979) estimated that 7% of interactions between *P. californicus* workers from different colonies resulted in mortality. (3) Navigation failure may also contribute to forager mortality. We could not find data to support this hypothesis, but navigation failure resulting in one lost forager every 300 foraging trips could account for approximately half of the mortality observed for *P. owyhee* (assuming a 14 day life expectancy and 10 trips/day/forager, De Vita 1979; Rogers 1974). (4) Extreme environmental stress associated with long foraging trips on sunbaked desert pavement may also contribute to high forager mortality (Whitford et al. 1975). Workers so stressed may simply 'wear out' because colonies do not produce foragers capable of indefinitely tolerating physical abrasion, high temperatures and low humidities. The actual causes of forager mortality are probably a combina-

tion of several factors and undoubtedly vary with location and season.

Given that 9.1% of a *P. owyhee* colony forages (Table 1), with a 2.5-month foraging season a 14-day forager life expectancy translates into a worker mortality rate of 0.7% per day and 49% per season. An apparent conclusion of these results is that much of the interior worker population must act as a reservoir for replacing short-lived foragers. This worker reservoir is especially important in view of observations that most of a given year's brood does not forage until the following year (unpublished data) and therefore cannot normally replace forager losses. These data may also explain why Wilson (1968) observed that *P. badius* workers were 'idle a seemingly unconscionable amount of time' since inactivity would be adaptive among interior workers acting as a reservoir for the foraging population.

The presence of a large reservoir of interior workers may also be an important factor limiting the evolution of physical castes. Oster and Wilson (1978) estimated that ant colonies perform 20–35 different tasks; of these, well over half are performed within the nest. In situations where foraging conditions require a large reservoir of forager replacements, it would often be more efficient to rely on this standing population of otherwise inactive workers to perform interior tasks than it would be to develop physically specialized interior workers. The high cost of producing such interior castes may simply not justify their increased efficiency if workers already in the forager reservoir could perform the same tasks. Wilson (1968) modeled an analogous situation by illustrating how evolutionary increases in the population size of one caste can lead to the extinction of a second more specialized caste. One would predict that the evolution of specialized interior castes would be inhibited by large populations of reserve foragers.

A Disposable Forager Strategy. Social structure of *P. owyhee* seems adapted to tolerate high forager mortality by utilizing disposable foragers. Starvation mortality (Fig. 4) and dry weight data (Fig. 3, Table 2) suggest that energy reserves accumulate in the interior worker populations and decline as ants progress to foraging. The picture that emerges is that interior workers are a reservoir of both colony energy and forager replacements; they are large in population size, long lived and high in energy reserves. In contrast, foragers are low-cost investments in food gathering; they are physically worn, few in number, short lived and drained of most energy reserves. Important advantages of this strategy are: (1) less colony energy would be lost to predation and other mortality factors, and (2) fewer specialized predators could sur-

vive because less energy would be available in their prey base.

Why has *P. owyhee* developed a disposable forager strategy? Even though this strategy minimizes costs of high forager mortality, the production of workers necessary to sustain this system makes it a high cost investment in food gathering. The reason is probably threefold: (1) this ant harvests seeds which are abundant and high in energy, (2) colonies of this species are 'apparent' food sources subject to high predation, and (3) their inability to eliminate predation and other possible sources of mortality may make toleration of high forager mortality an expedient strategy, especially when the energy supply is sufficient to allow ready replacement of lost workers.

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